A seasonal application of the GAMS (1932) method, modified MICHALET (1991): the example of the distribution of some important forest species in the Alps

Gilles Pache, Richard Michalet & Serge Aimé

Abstract

The authors present a seasonal application of the Gams method. The first section describes two maps illustrating summer and winter Gams indices over the southern half of France. Here the separate effects of aridity and continentality on the climate of this region are demonstrated. In the second section, a biological application of the method in the Alps, the French Pyrenees and the Massif Central is illustrated by a study of the bioclimatic distribution of five fundamental forest species of the montane and subalpine belts. The synthesis of these results along three transects crossing the Alps, allows to understand the respective influences of aridity and continentality on the phytoclimatic organization of the Alps. The important divergences in the biological composition of the western (France and Switzerland), and the eastern (Italy) parts of the chain are thus clearly explained.

Key words: Alps, continentality, forest vegetation.

Acronyms: A: altitude, P: rainfall, Ga: Gams annual index, Gs: Gams summer index, Gw: Gams winter index, Gvp: growth vegetation period index (April to August,) m: average winter temperatures minima (December, January and February).

Résumé

Application saisonnière de la méthode de GAMS (1932), modifiée selon MICHALET (1991): distribution de quelques espèces forestières dans les Alpes.

Les auteurs présentent une application saisonière de la méthode de Gams. La première partie consiste en une description de cartes des indices de Gams estivaux et hivernaux couvrant la moitié sud de la France. Les influences respectives de l'aridité et de la continentalité sur le climat de cette région sont ainsi expliquées. Dans la seconde partie l'intérêt biologique de la méthode est abordé par l'étude de la distribution bioclimatique de cinq espèces forestières fondamentales des étages montagnard et subalpin des Alpes, des Pyrénées françaises et du Massif Central français. La synthèse de ces résultats, le long de trois transects représentatifs de la chaîne alpine, permet de saisir les influences respectives de l'aridité et de la continentalité sur l'organisation phytoclimatique des Alpes. Les importantes divergences existant entre les compositions biologiques des versants occidentaux (français et suisse) et orientaux de la chaîne (Italie) sont ainsi clairement expliquées.

Mots-clés: Alpes, continentalité, végétation forestière.

Abréviations: A: altitude, P: précipitations, Ga: indice annuel de Gams, Gs: indice estival de Gams, Gw: indice hivernal de Gams, Gvp: indice pour la période de végétation (avril à août), m: moyenne des températures minimales en hiver (décembre, janvier et février).

1. Introduction

The classical distinguishing feature of the vegetation which divides the Prealpine girdle from the intra-alpine axis is the absence of beech (*Fagus sylvatica* L.) in the intra-alpine areas. GAMS (1932) used a precipitation continentality index to correlate such botanical observations with a decrease in the altitudinal pluviometric gradient with continentality. This index is expressed by an angle with low values in oceanic massifs (< 35°) and high values in continental areas (> 55°) as seen on figure 1. This method is most efficient for comparing the climates of stations situated at different altitudes because the index is not dependant on altitude but only on the altitudinal pluviometric gradient of the stations. It was applied to the entire Alps by OZENDA (1966, 1981 and 1985), RICHARD & PAUTOU (1982) and RICHARD (1985). Recently, one of us (MICHALET, 1991a) introduced a modification which allows a more effective application of the method at low altitudes (see fig. 1).

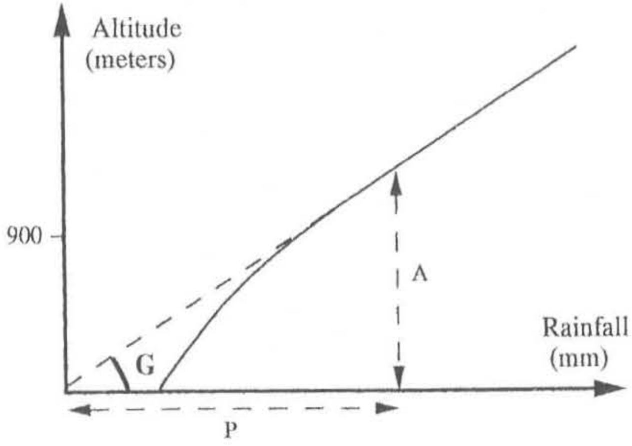


Fig. 1. — Precipitation continentality index:

- if A > 900 m: $\text{cotg}\ G = P/A$ (GAMS, 1932)

- if A < 900 m: $\text{cotg}\ G = \dfrac{P - \dfrac{900 - A}{100}\,\dfrac{P}{10}}{A}$ (MICHALET, 1991)

The full curve shows the real increase of rainfall (with increasing altitude) in a given mountain, and the dashed line shows the modified curve which is created under 900 m by the modified index, to make values theoretically comparable at all altitudes.

Concerning the appelation of the index, "precipitation continentality coefficient", RICHARD (1985) emphasized that there is not always a true continental climate in the inner Alps. Conversely, IZARD & al. (1985) demonstrated that some peripheral areas of the Pyrenees are really subject to continental climates. In fact, an increase of the Gams angle in a massif corresponds whith orographic sheltering from the general climate which can just as well be either oceanic, Mediterranean or even continental. For the above reason we now use the name "index of relative precipitation continentality" for Gams angle in this context (MICHALET, 1990 and 1991b).

The seasonal variations in rainfall distribution in the range of the Alps emphasize an important flow inherent in all climatic indices using annual rainfall averages. This is illustrated by the fact that equally high annual Gams angles could either be due to a winter precipitation deficit in a continental area, as in the eastern Alps, or to a summer deficit in a Mediterranean area, as in the southern Alps. Since differences like these are biologically decisive, the use of annual indices must be limited to areas where the seasonal rainfall distribution is quite homogeneous.

For the extension of the index to large areas like the Alps, we suggest using *seasonal indices* :

- a summer angle (Gs) showing the horizontal variations of aridity in relation to the altitude of the concerned stations;
- a winter angle (Gw) allowing to the identification of stations characterized by an important continentality (low precipitation in winter) or oceanic influence (important precipitation in winter).

In the first part of this paper we present the results of a cartographic application of the two seasonal Gams indices over the southern half of France (PACHE, 1991). In the second, part we examine the biological utility of the method by means of an analysis of the bioclimatic distribution of five forest species which are characteristics of the montane and subalpine belts of the entire Alps: beech (*Fagus sylvatica* L.), fir (*Abies alba* Mill.), spruce (*Picea abies* (L.) Karst.), larch (*Larix decidua* Mill.) and scots pine (*Pinus sylvestris* L.). The synthesis of these results in three bioclimatic transects gives possible explanations for the phytoclimatic organization of the Alps. This scheme is then compared with the classic distinctions made between the Prealpine girdle and the intra-alpine axis. We conclude by discussing the biological applications and limitations of the method.

2. The climatic map: distribution of the seasonal indices

2.1. The climatic stations and the method

The maps (fig. 2A and 2B) are limited to the southern half of France, which includes three mountain ranges: the Alps, the Pyrenees and the Massif Central. This area is largely subject to temperate oceanic and Mediterranean climates (the two dominant climates of Western Europe). 780 stations have been used, of which 725 have non-interrupted data for the period 1951-1980, and of which 45 have at least 15 years of non-

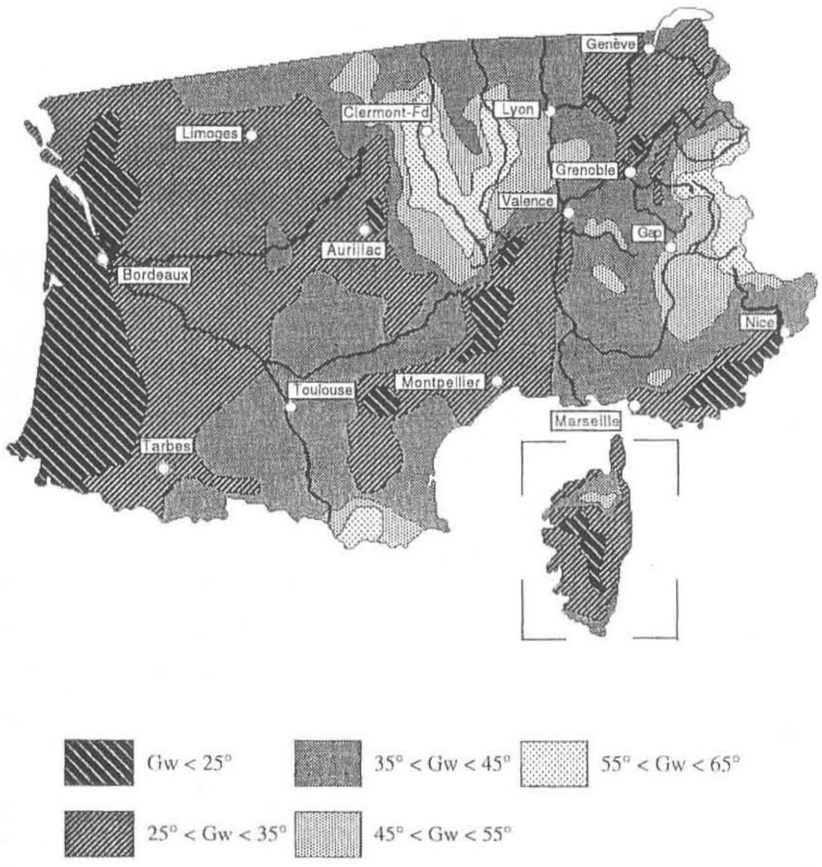


Fig. 2A. — Distribution of the seasonal Gams indices in the southern half of France: winter index (Gw)

interrupted data during the same period. All the data are from the DIRECTION DE LA METEOROLOGIE NATIONALE FRANÇAISE (1986). The seasonal figures has been multiplied by four to make values comparable with annual indices. Indices have been calculated using the classic GAMS method (1932) for the stations above 900 m and with the modified method (MICHALET, 1991a) for the lower altitudes as described above.

2.2. *The spatial variations of the winter index*

The Gams angle domains < 35°, characterized by their very wet winter involve four zones which can be sub-divided into two sectors, according to the origin of the atmospheric disturbances:

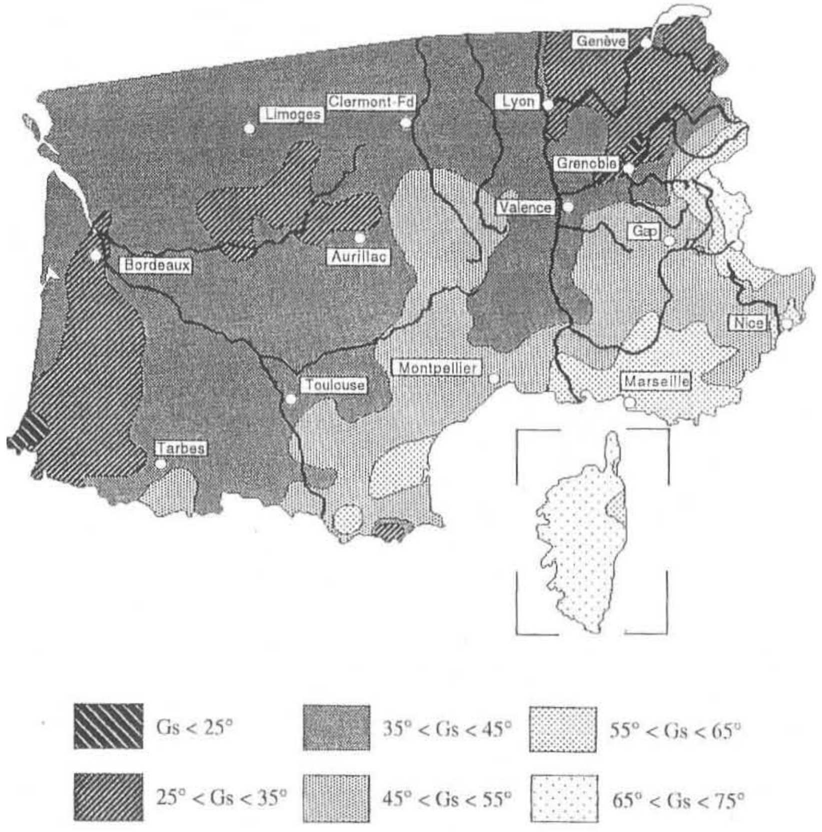


Fig. 2B. — Distribution of the seasonal Gams indices in the southern half of France: summer index (Gs)

- A western sector which includes the Atlantic front and the western periphery of the Pyrenees and of the Massif Central, as well as the foothills of the Alps from the southern Jura to the southern Vercors. In these areas, the atmospheric disturbances come from the west, and their influence is clearly oceanic (DAUPHINE, 1976).
- A southern sector which includes the Mediterranean littoral from Italy to Marseille and almost the whole of Corsica, plus the southern and eastern periphery of the Massif Central. In this case, the atmospheric disturbances come from the Mediterranean sea, especially the gulf of Genoa. Therefore, the oceanic characteristic of those heavy winter rainfall is not classically recognized.

The domain 35-45° slots in between the preceding zones and the fairly sheltered areas of the following domains. It is very limited in the mountains, but spreads out extensively in the plains, e.g. north of the Massif Central or around Toulouse.

The domains 45-65° correspond to rather sheltered areas which exist only in the main massifs (Massif Central, Pyrenees and Alps). The classic intra-alpine areas from the Haute-Tarentaise to the Haute-Tinée, and in the Pyrenees the inner core of Cerdagne and the peripheral massif of Canigou, where climate is truly continental, are included in this domain. In the eastern Massif Central, the sheltered valleys of the Allier and the Loire behind the volcanic massifs are also characterized by true continental influences. In Corsica, there is a small internal zone in the northern Cinto in the "désert des Agriates".

2.3. The spatial variations of the summer index

The domains < 35° characterized by a very rainy summer exist only in peripheral massifs where winter is also very oceanic (western Pyrenees, western Massif Central and northern Alps). This orographic effect, which is nevertheless more significant in winter, increases the rainfall all year round. The presence of the domain 25-35° around the Canigou (Pyrenees) is, on the contrary, dependant on the continental characteristic of the climate of this massif.

The domain 35-45° is the most prevalent summer domain. It characterizes the temperate and non Mediterranean zones of France.

The domains 45-55° and 55-65° characterize the classic submediterranean (45-55°) and Mediterranean (55-65°) areas such as the Mediterranean coast and its interland, but they are also common in the well sheltered mountains also characterized by a high winter index (Cerdagne, south-eastern Massif Central, inner Alps and south-western Alps). In the same way that the characteristic oceanic climate of the peripheral massifs increases the summer rainfall, the continental characteristic of the well sheltered areas decreases their summer rainfall. The result is in a summer convergence between the continental areas and the Mediterranean areas which are often characterized by an oceanic winter.

The domain 65-75° is prevalent in Corsica. This is a zonal characteristic depending on the southern location of the island which makes it comparable to other Mediterranean areas situated at a same latitude (central Spain and central Italy, Balearic islands and Sardinia). The presence of this domain in the Haute-Durance and the Haute-Ubaye shows the aridity of these inner valleys relatively to their altitude.

2.4. Conclusion

This cartographic approach provides very different informations according to the season under consideration.

The winter index is directly connected to the atmospheric disturbances affecting the studied region. We believe that the low winter indices represent the oceanic characteristic of the climate whether perturbations come from the Atlantic ocean or the Mediterranean sea. On the contrary, the high winter indices characterize a precipitation continentality which is either absolute in the case of a true continental climate (massif of Canigou), or relative for the fairly sheltered areas (Inner Alps, Cerdagne, eastern Massif Central).

The summer index emphasizes the zonal succession from north to south depending on the summer ascent of the anticyclone of the Azores:

* a temperate zone : Gs < 45° (most of the map);
* a submediterranean zone: 45 < Gs < 55° (the Provence hinterland);
* an attenuated Mediterranean zone: 55 < Gs < 65° (the Mediterranean coast);
* an average Mediterranean zone: 65 < Gs < 75° (Corsica).

Remark: the accentuated Mediterranean zone characterized by an index greater than 75° is present in North-Africa.

This zonation is disturbed in the sheltered areas which have a similar summer rainfall deficit as the zonal Mediterranean areas, even though they are situated at a temperate latitude. However, the drought characterizing the real Mediterranean stations (P < 2T) does not appear in those areas because of their higher altitudes (> 1000 m). In other respects, the Mediterranean climate is not only characterized by its aridity but also by its mildness.

3. Correlations with the distribution of forest species

3.1. Method

To evaluate the biological implications of the preceding climatic divisions, we will attempt to correlate the presence or the absence of five forest species, which are representative for both the mapped zone (fig. 2) and the entire Alps, with the seasonal Gams indices data. Various vegetation maps, particularly those with large scale (1/50 000 to 1/200 000) have been examinated. It is clear that the observed presence or absence of a species depends on the scale of the map used. In order to overcome resultant inaccuracies, a large number of climatic stations have been used.

The interpretation process is the following. When a species is always present or absent in certain climatic conditions, a climatic explanation is favoured. If there are only a few exceptions to the rule, this could be due to human factors. However, this could be due also to the fact that the species has not yet reached some areas where it is able to live since the end of the Würm glaciation. When a species is about as often present as absent for a specific climatic condition, human activities are considered to be the most likely explanation.

For some species, we have applied another relative precipitation continentality index which includes the months from April to August. This new index, called Gvp, is more representative of the growth vegetation period than Gs. For beechs, we have also studied the influence of low winter temperatures using the average of the minima of December, January and February. For this correlation, only stations with an altitude compatible with the presence of beech have been used, i.e. approximatively 600 to 1400 m when located north of 46th parallel, and 900 to 1700 m south of this latitude. To save space in the bibliography, all the maps used are not cited. The climatic data used come from FLIRI (1975) for Austria, Ministerio dei Lavori publici (1957) for Italy and UTTINGER (1966) for Switzerland.

3.2. Fagus sylvatica L.

The figure 3A illustrates the climatic distribution (Gw/Gs) of beech in more than 400 stations located in the Alps, the French Pyrenees, the Massif Central and Corsica. From this, it can be deduced that beech is absent for winter Gams indices over 68°, corresponding to stations in the inner Tyrolean Alps (Austria and Italy) , and some upper valleys of the Piemont (Italy). Beech is also very rare for summer Gams indices over 60°, except in some Italian valleys (Piemont) and in Corsica.

The figure 3B (Gw/Gvp) illustrates for the same stations the importance of the spring rainfall which can attenuate the summer drought. Here, beech is absent for Gvp indices over 60°. However, in many northern stations, beech is absent even when the preceding parameters are in its favour.

The figure 3C examined the effect of low winter temperatures and shows that beech is absent when m (average winter temperatures minima) is approximately less than -7°C. The few absences in stations where the above mentioned climatic parameters are nevertheless favourable, such as those in the French Alps, are attributed to human interference. This hypothesis was proposed by BARBERO & al. (1973) in the massif of Mercantour where beech is only present in the ancestrally preserved forest of Peira-Cava.

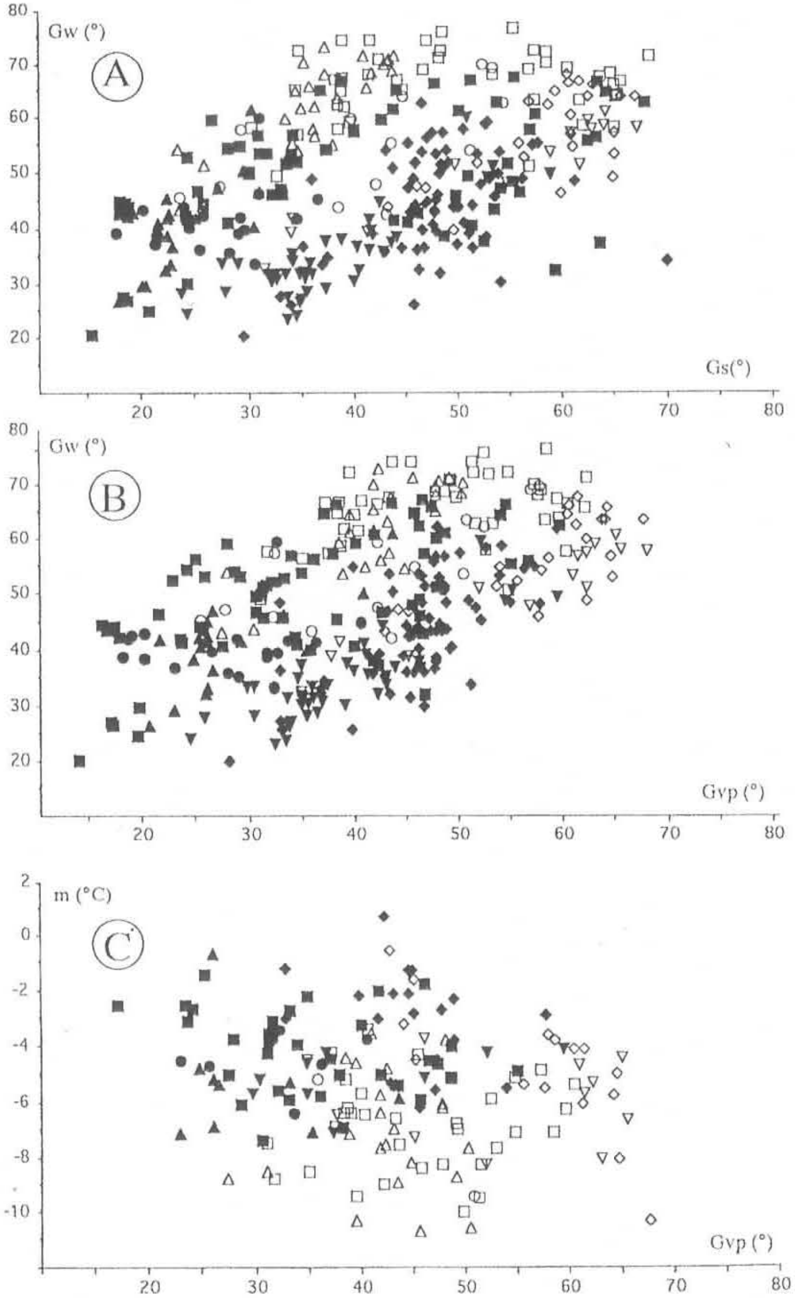


Fig. 3. — Relationship between the presence (full symbols) or the absence (open symbols) of beech (*Fagus sylvatica* L.) and the climate of the stations (3A: Gs/Gw, 3B: Gvp/Gw, 3C: Gvp/m). French stations (▼ northern Alps, ◆ southern Alps), ▲ Austrian stations, ● Swiss stations, ■ Italian stations.

3.3. *Abies alba Mill.*

Figures 4A and 4B shows that fir is always absent from the stations characterized by winter indices approximatively over 65°, conditions which only exist in the Tyrolean Alps and in the Piemont, not in the French Alps. In contrast to beech, its presence in stations characterized by dry summers cannot be explained by the heavy spring rainfall because it is even present when Gvp indices almost reach 70° (fig. 4B).

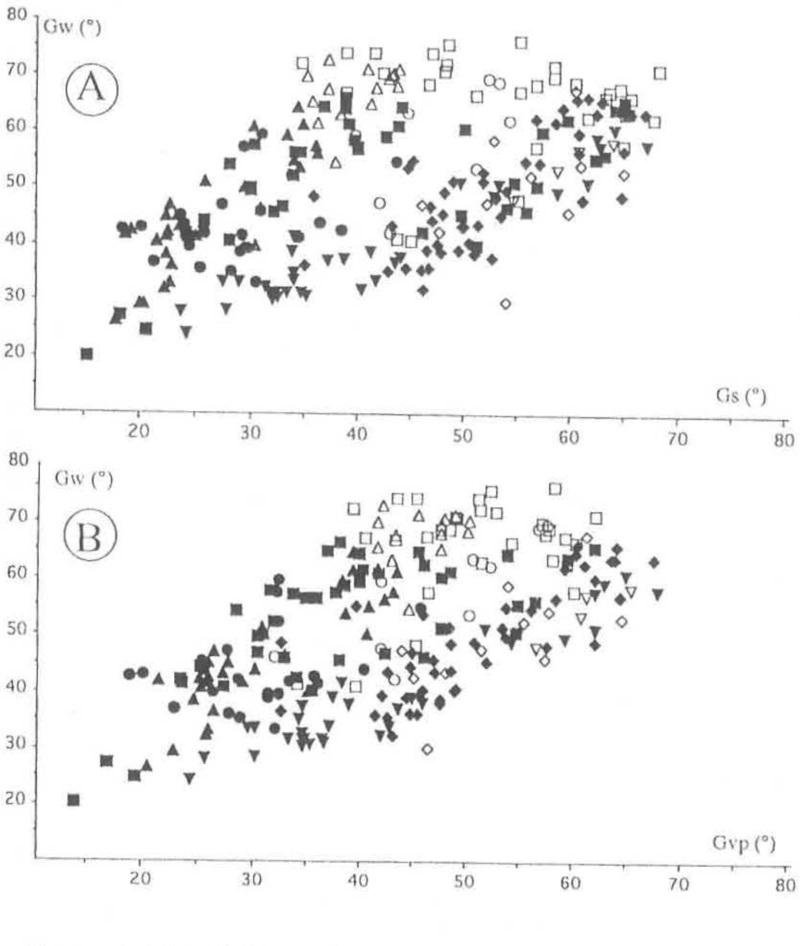


Fig. 4. — Relationship between the presence (full symbols) or the absence (open symbols) of fir (*Abies alba* Mill.) and the climate of the stations (4A: Gs/Gw, 4B: Gvp/Gw). French stations (▼ northern Alps, ◆ southern Alps), ▲ Austrian stations, ● Swiss stations, ■ Italian stations.

However, all the stations with Gvp values over 60° are subalpine fir forests, because of the high tolerance to low winter temperatures of the species compared to beech. So, there is no fir in the montane belt when Gvp values are greater than 60°, and the species is also absent in the south facing slopes when Gvp values exceed approximatively 40°.

The absence of subalpine summits may explain the absence of fir in localities in the southern French Alps where Gw is much lower than 65° (fig. 4B), given the relatively high Gvp values. On the other hand, in some localities of the Piemont, north of the col de Tende, the absence of climatic explanation suggests some human interference (BONO & BARBERO, 1976; BARBERO & OZENDA, 1979).

3.4. *Larix decidua Mill.*

On figure 5, the distribution of larch appears to depend totally on the winter index because of the general absence with values under about 45°. Even though the summer index (and also Gvp) does not seem to be determining factors, it is certain that larch is limited to north facing slopes and nearly always in the subalpine belt for localities with high summer indices like in the Briançonnais (FOURCHY, 1951; CADEL, 1980). Conversely, larch can be abundant right down to the hill belt in areas with wet summers, e.g. in northern Austria (MEISEL & al. 1984) or in Ticino (SCHMID, 1939-1950).

In spite of the fact that the distribution of larch appears to be solely dependant on climatic parameters, many authors have demonstrated that

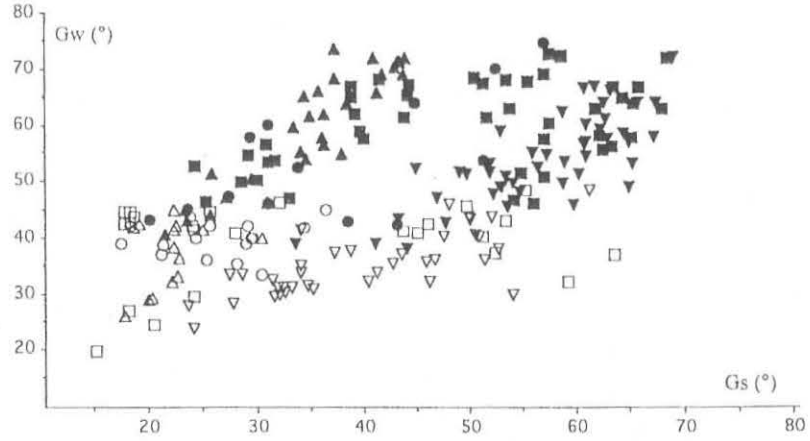


Fig. 5 — Relationship between the presence (full symbols) or the absence (open symbols) of larch (*Larix decidua* Mill.) and the climate of the stations (Gs/Gw). ▼ French stations, ▲ Austrian stations, ● Swiss stations, ■ Italian stations.

its abundance relies on human interference. For example, in similar climatic conditions, in the French Alps, larch can be either very abundant like in the Briançonnais (CADEL, 1980), or thinly scattered in the arolla pine forests like in the Maurienne valley (BARTOLI, 1966), depending on the extent of human interference.

3.5. *Picea abies (L.) Karst.*

The three following figures concern the distribution of spruce. Figure 6 represents the subalpine forests, whereas figures 7A and 7B represent the montane spruce forests. In the subalpine belt (fig. 6), spruce can grow in all the studied climatic conditions, even at extremely high Gvp values not represented here. In contrast, in the montane belt spruce is absent when Gs is above about 62° (fig. 7A); Gvp turns out to be less explicative (fig. 7B). Therefore, summer aridity seems to limit spruce whilst Gw is not a decisive factor as in the case of fir.

Nevertheless, spruce is absent in many southern localities (Piemont Alps and southern French Alps) where the climatic conditions seem to be favourable to the species, i.e. for Gs between 45° and 62°. De BEAULIEU (1978) and OZENDA (1981) emitted the hypothesis that the postglacial migration of the species from east to south has not been yet completed. It is thought that the human interference could also account for this solution because of the abundance of spruce in the Massif of Mercantour which is the most meridional of the entire Alps.

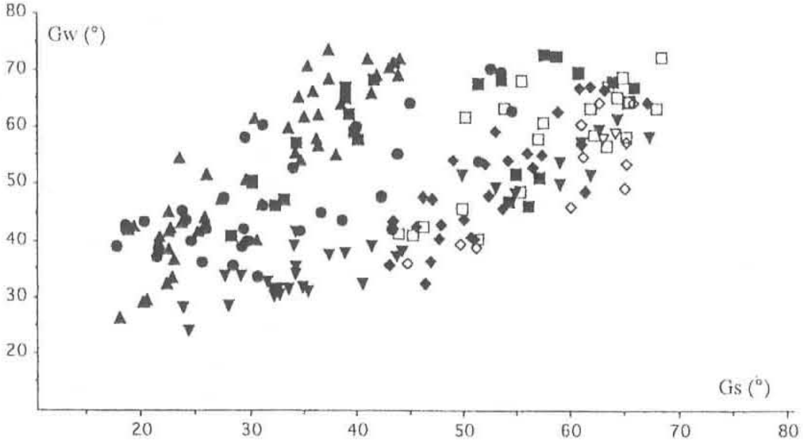


Fig. 6 — Relationship between the presence (full symbols) or the absence (open symbols) of subalpine spruce (*Picea abies* (L.) Karst.) and the climate of the stations (Gs/Gw). French stations (▼ northern Alps, ◆ southern Alps), ▲ Austrian stations, ● Swiss stations, ■ Italian stations.

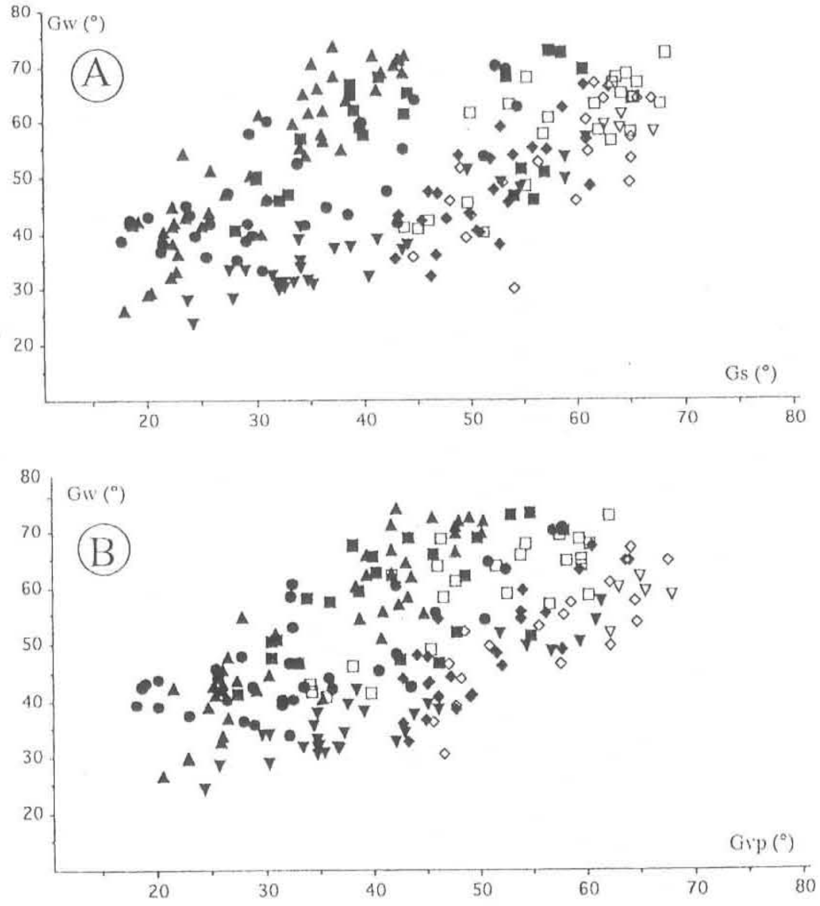


Fig. 7 — Relationship between the presence (full symbols) or the absence (open symbols) of montane belt spruce (*Picea abies* (L.) Karst.) and the climate of the stations (7A: Gs/Gw, 7B: Gvp/Gw). French stations (▼ northern Alps, ◆ southern Alps), ▲ Austrian stations, ● Swiss stations, ■ Italian stations.

3.6. *Pinus sylvestris L.*

Scots pine does not seem to be influenced by Gs and Gw (fig. 8A), but is always present when Gvp is over 60° and nearly always when Gvp is above 50° (fig. 8B). Between about 40 and 50°, this species is common, but it is rare when Gvp is inferior to 40°. In fact, scots pine can endure all the precipitation conditions, but its presence, and more precisely its abundance, depends on the absence of competing montane species, the absence of which in turn depends on the climatic conditions and the extent of human interference (RAMEAU, 1987).

At the montane level, for Gvp over 60°, beech, fir and spruce are always absent; so scots pine is the potential climax species, excepted on north facing slopes where larch is often present. This includes scots pine forests from Cerdagne (French Pyrenees), French inner Alps (especially the Maurienne valley and the Briançonnais), and some valleys of the Piemont (especially Susa and Aosta).

When Gvp is approximatively between 40 and 50°, and up to 60° on north facing slopes only, scots pine has colonized the abandoned pasture land where, originally, spruce, beech or fir were abundant. The *Erico carneae-Pinetum sylvestris* Br.-Bl. 39 in the eastern Alps (MAYER, 1974), in many valleys of the Piemont Alps (BONO & BARBERO, 1976), and the mesophilic *Pinus sylvestris* series from the French Alps, and the Massif Central (OZENDA & LUCAS, 1987) are generally such paraclimacic scots pine forests.

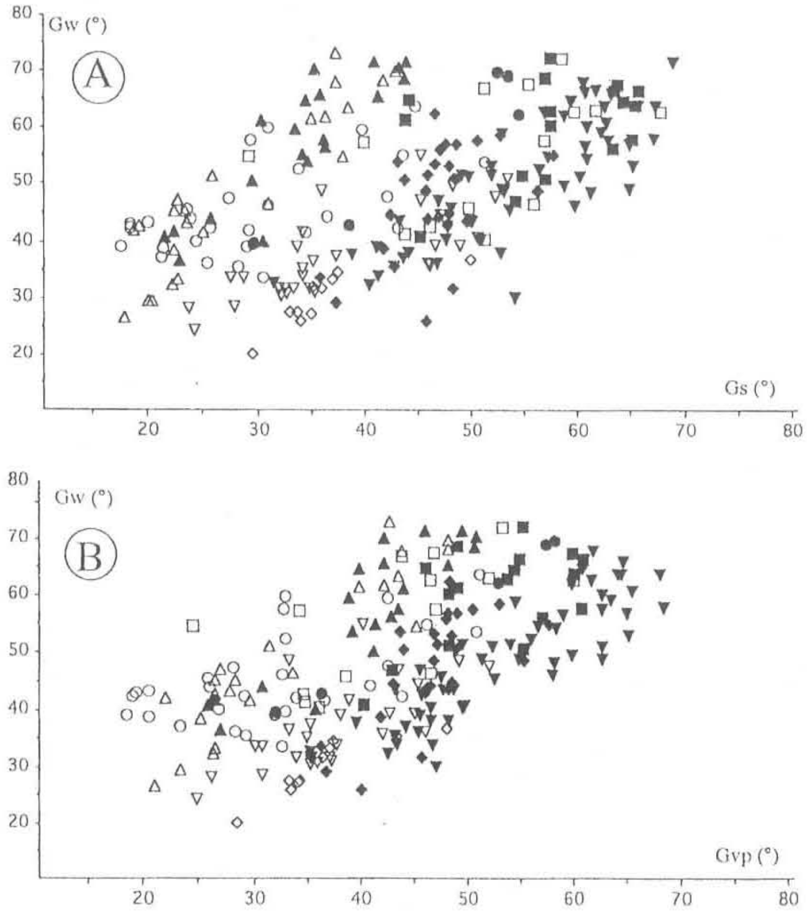


Fig. 8 — Relationship between the presence (full symbols) or the absence (open symbols) of scots pine (*Pinus sylvestris* L.) and the climate of the stations (8A: Gs/Gw, 8B: Gvp/Gw). French stations (▼ from Alps, ◆ from Pyrenees and Massif Central), ▲ Austrian stations, ● Swiss stations, ■ Italian stations.

When Gvp is below approximatively 40°, other species are very dynamic and recolognize directly the abandoned farm land, except in very harsh edaphic conditions where scots pine prevails.

3.7. Conclusion

The above mentioned results indicate that each forest species has its own climatic limitations :

- fir is absent from the most continental areas (Gw > 65°);
- on the contrary, larch is absent from the most oceanic massifs (Gw < 45°);
- beech shows three limitations: the winter cold (m < -7°), drought during the vegetative period (Gvp > 60°), and to a lesser extent the winter precipitation continentality (Gw > 68°);
- spruce is not very tolerant to summer aridity, but its thermal plasticity enables it to grow in subalpine areas when Gs is high, what is also the case for fir and larch when Gvp is too high;
- scots pine is the most indifferent to climatic conditions, its presence depending on the absence of competitors.

4. Distribution of forest species along three transects across the Alps

Three prevalent climatic influences hit the Alps: oceanic temperate in the north-west, continental temperate in the east and Mediterranean in the south. However, as one penetrates into the chain, several transitional sub-types of these pheripheral climates are induced by the resultant sheltering effect. Each part of the chain is characterized in this way by a unique arrangement of the thermal and rainfall variables. Therefore, various combinations of tree species exist, depending on the contrasting climatic requirements and limitations of the individual species.

Using three bioclimatic transects representative of the main types of alpian climates, an attempt is made to explain the observed vegetation patterns (fig. 9).

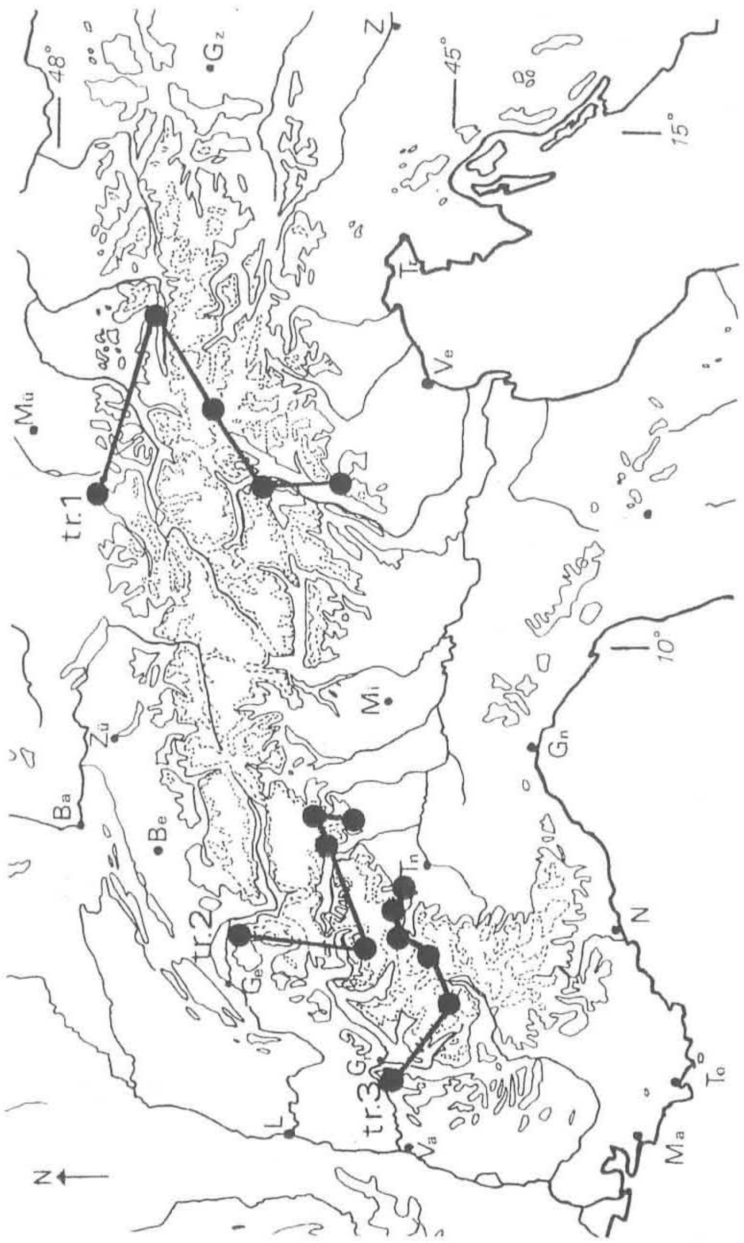


Fig. 9. — Localization of three transects in the Alps (Ba = Basel, Be = Bern, Ge = Genève, Gn = Genova, Gr = Grenoble, Gz = Graz, L = Lyon, Ma = Marseille, Mi = Milano, Mü = München, N = Nice, Tn = Torino, To = Toulon, Tr = Trieste, Va = Valence, Ve = Venezia, Z = Zagreb, Zü = Zürich).

4.1. Method

For each transect we have chosen five or six localities at an altitude of about 1000 m. Together, they represent the two external zones, the two intermediate zones and the one or the two inner zones which are classically recognized by biogeographers (MAYER, 1974; OZENDA, 1981; RICHARD & PAUTOU, 1982).

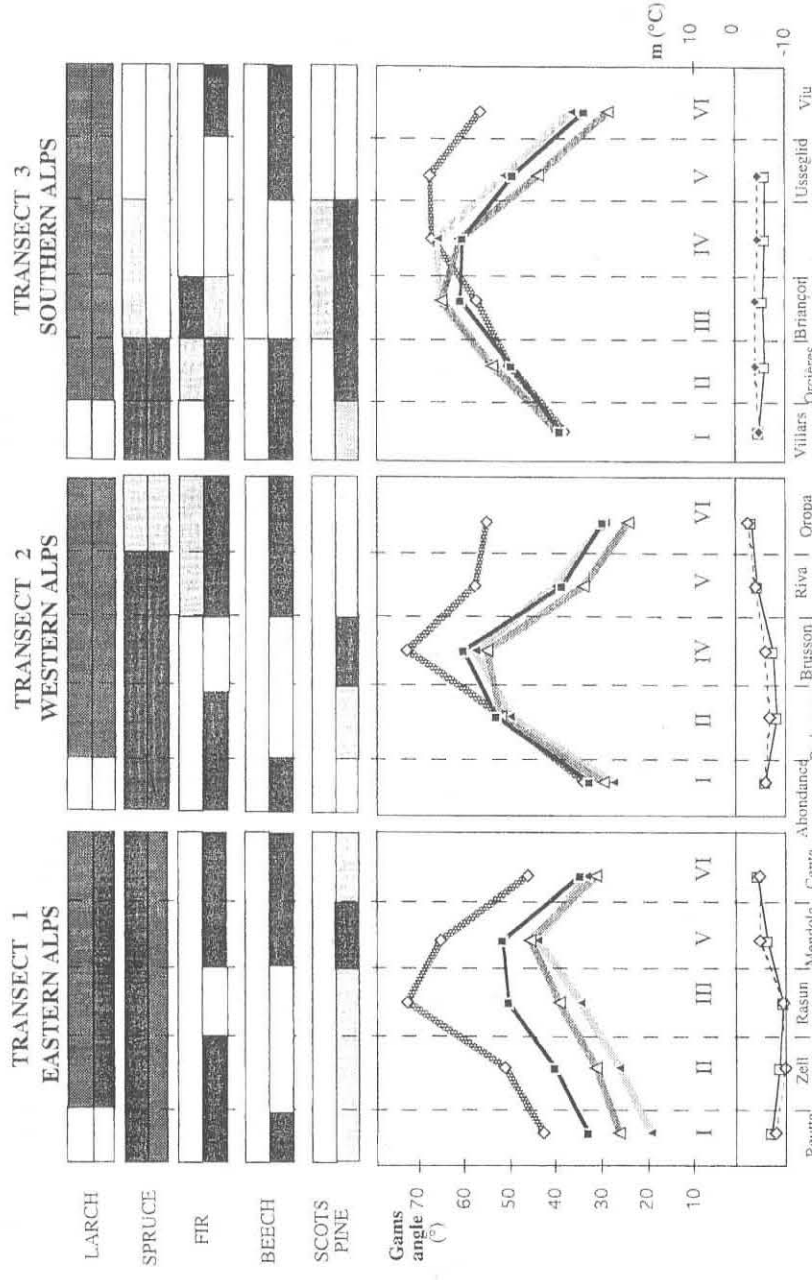
In figure 10, the top of the figure illustrates the occurence of the five tree species in the montane and subalpine belts for each transect. The climatic variable data are indicated below. The classic annual Gams indices (Ga) are also indicated for use in reference to previous works. In addition to the minimum winter temperatures of the localities, a minimum winter temperature was calculated at 1000 m above sea level for a better comparison, based on the assumption that there is roughly a 0,5°C drop in temperature for each 100 m increase in altitude for the southern French Alps (AIME & SARRAILH, 1974; DOUGUEDROIT & SAINTIGNON, 1970).

4.2. The eastern Alps

(fig. 10, transect 1)

In a north to south direction, this transect crosses the Bavarian Alps in the external zone (Reutte, I), the Kitzbühel Alps in the intermediate zone (Zell am See, II), the inner Tyrolean zone near Bruneck (Rasun di Sotto, III), the southern intermediate zone near Bolzano (Mendola, V) and the external zone of Trento (Centa, VI). There is a high precipitation continentality in winter in the inner zone (Gw > 70° in III) and low winter temperatures only in the northern part of the transect (m about -10°C in II and III). However, there is little summer drought as Gs does not rise above 45°, even in the driest zone (V).

The low Gs data explain the abundance of spruce throughout the transect. Larch is also common, even in the southern external zone (VI); it is only absent in the northern external zone which is a little too oceanic (Gw approximately 42° in I). Fir is excluded from the inner zone which is too continental (Gw near 72° in III) and beech from the northern intermediate zone which is too cold (m < -7°C in II). Scots pine is common on south facing slopes of the dry southern intermediate zone, which suffers most from human interference. However, it is scarce elsewhere even in the inner zone where spruce is common. The limiting factors for scots pine here are either edaphic or anthropic (PITSCHMANN & al., 1970; SCHIECHTL & STERN, 1976).



4.3. *The north-western Alps*
(fig. 10, transect 2)

The transect starts in the west in the French external zone (Abondance, Haute-Savoie, I), then crosses the Tarentaise valley in the intermediate zone (Pralognan, II), the inner zone in the Aosta valley (Brusson, IV), the eastern intermediate zone (Riva Valdoblia, Val Sesia, V), and finally the external zone in the Bielese Alps (Oropa, VI). The climatic conditions in winters are very different in the two external zones, oceanic in the west (I), continental in the east (VI). It is also colder in the west than in the east because of the influence of the Po valley in the east. As shown in the preceding transect, the sheltering effect has more influence during winter, Gw reaching 72° in the inner zone (IV). Summer and especially spring (Gvp < Gs) remain wet in the east, but not in the west. The winter is not as cold as in the eastern Alps (m near -6°C).

Spruce is a dominant species, except in the Italian external zone (VI) where it is absent from some valleys, maybe for chorologic reasons. Larch is absent from the too oceanic western external zone (Gw about 32° in I). Fir, absent from the inner zone (Gw about 72° in IV), reaches the subalpine belt in the east, maybe because of the warmer temperature and the rarity of spruce. Beech is absent from the western intermediate zone (II) because of thermic limitations. These are due to the high altitude of the valleys as opposed to the massif being a particulary cold one (m about -6°C at 1000 m). Scots pine, which is a climax species on the south facing slopes of the Aosta valley (Gvp near 58° in IV), is not abondant in the western intermediate zone (II), where spruce, fir and larch are common. It is quite absent from the other areas.

4.4. *The southern Alps*
(fig. 10, transect 3)

This transect starts in the Vercors (Villars de Lans, I) in the western prealpine foothills, then crosses the massif of Oisans in the intermediate zone (Orcières, Haut-Drac, II) and in the French inner zone (Briançon, III). In Italy the transect crosses the inner zone in the valley of Susa (Bardonecchia, IV), then follows the Stura of Viu in the intermediate zone (Usseglio, V) to reach the external zone at Viu (VI). There is

Fig. 10. — (left page) The three transects crossing the Alps.
Occurence of the species in the montane (1st line) and subalpine (2nd line) belts
▓ important presence of the species
░ sporadic presence of the species
Climatic indices: ◇ Gw ▲ Gs △ Gvp ■ Ga
□ winter minimum - - ◆ winter minimum extrapolated at 1000 m above sea level
I and VI: external zones, II and V: intermediate zones, III and IV: inner zones

always a high precipitation contrast between the two external zones in winter: oceanic in the west (I) and very continental in the east (VI). The submediterranean influence, which is perceptible in the two external parts of the transect (Gs about 40° in I and VI) is compensated in the east by high spring rainfalls (Gvp < 30° in VI). The sheltering effects increase these divergences, and in the western inner zone Gs data are higher (65° in III) than those of the French Mediterranean coast (fig. 2B). In the east, Gs values are also high because of the meridionality, but Gvp is below 45° in the intermediate zone (V) when Gw is always very high. The winter is not cold over the whole transect, with m around -4°C at 1000 m.

Fir is always present at the subalpine belt in the western inner zone (Gvp = 64° in I) which is oceanic enough for it (Gw < 58°), whereas it is absent in the eastern intermediate zone, which is wet enough during the growth vegetation period (Gvp around 43° in V), but too continental (Gw about 67°). Beech is present in the two intermediate zones (II and V) which are not very cold, but it cannot grow in the two inner zones because they are too dry (Gvp > 60° in III and IV). Scots pine, which is present on south facing slopes of the western intermediate zone (II), is a dominant species in the montane belt of the two inner zones (III and IV), where it is free of competitors. Further east, beech and larch limit this species, even in the intermediate zone (Gvp around 43° in V). Spruce, still present in the west, is very rare in the inner zones (III and IV), where it is limited to the subalpine belt. In the east (V and VI) its total absence is certainly chorologic (BARBERO & OZENDA, 1979) or due to human influence. Larch, common in all the eastern zones, is not able to colonize the western external zone as it is too oceanic (Gw near 38° in I).

4.5. Discussion

The comparison of the three transects in figure 10 illustrates the extensive forest heterogeneity whithin each zone type (external, intermediate and inner) as one crosses the Alps:

- larch, absent from the western external zones, is always present in the eastern external zones where it mixes with beech, fir and spruce;
- fir, absent from the eastern inner zones, is present in the subalpine belt of the south-western inner zone (Briançonnais) even though it is the driest one of the entire Alps;
- scots pine, an abundant and potential climax species in the western inner Alps, is sporadic in the east where its presence is due to edaphic or anthropic factors;
- beech, strictly limited to the external zone in the north-western Alps (transect 2) and the north-eastern Alps (transect 1), penetrates deep into both the valleys of Piemont and those of the southern French Alps up to the start of the inner zones.

These few examples illustrate that it is impossible to provide distinct biological criteria for the external, intermediate and inner zones of Alps. Indeed, such an approach should be limited to the scale of one part of the above mentioned transects, as demonstrated by CADEL & PAUTOU (1984) and PAUTOU & al. (1991) for the Dauphiné Alps, or FOURNIER & PELTIER (1987) for the Maurienne valley. Its generalization to the entire Alps (OZENDA, 1983, 1985) gives a limited view of the biological organization of the Alps and may be a source of confusion.

We have also demonstrated that it is impossible to use the annual Gams angle to justify the three subdivisions of the Alps. This criterion was first used for the alpine delimitation of the beech area (GAMS, 1932), while we have demonstrated that this species is limited mainly by temperature, not precipitation.

5. Conclusion

The seasonal use of the Gams method has two main applications.

Climatically, it provides a lucid distinction between the respective influences of precipitation continentality and aridity on a given area. Maps displaying the winter Gams angle illustrate both the precise origin of oceanic disturbances and also the sheltering effects of the orographic complexes which lead to continentalization of the climate. Variations of the summer Gams angle emphasize the climatic zonation depending on the annual ascent of the anticyclone of the Azores towards temperate latitudes. Nevertheless, the summer angle is also influenced by the sheltering effects, which may explain the aridity of some alpine valleys situated above Mediterranean latitudes.

Biologically, the separation of aridity from precipitation continentality is pertinent as they have contrasting ecological consequences. Excess in aridity for a plant corresponds to a deficit of precipitation during the growth vegetation period relatively to temperature. Except in the case of spruce, the summer Gams angle appears to be insufficient to characterize the water requirements of the studied forest species because spring precipitation can compensate for summer drought. The use of a Gams angle which includes also the months of April and May is most informative for these species, as they are all limited by water deficit during the growth vegetation period. However, because the contributions of precipitation are different for a given angle, depending on the altitude (and also temperature, orientation and soil) of the station under consideration, the Gams angle data threshold for a species varies according to the considered vegetation belt. In fact, species such as fir, larch and spruce, which can tolerate low winter temperature, climb to another belt to satisfy their water requirements when the Gams angle increases. Conversely, species such as beech, which are sensitive to the winter cold, are unable to move in a higher belt, and so their Gams angle thresholds are definitive.

Excess in precipitation continentality or oceanity for a plant appears to be rather dependant on the atmospheric environment of a massif, more precisely on the absolute humidity of the air. The winter Gams angle is most representative of this ecological factor and the data thresholds for the forest species appear to be independant on altitude. The distribution of fir and larch is strictly correlated with the winter angles. Fir avoids poles of continentality, and larch oceanic massifs.

These bioclimatic results emphasize the extensive variety in the climatic requirements of forest species and provide, in the Alps, an explanation for the species distribution patterns which have confused biogeographers for a long time. An example is the case of the beech-larch forests in the Italian Alps; these two species which seem clearly incompatible in the western Alps are closely mingled in the Italian Alps because the winter precipitation continentality is favourable for larch, whereas for beech, the growth vegetation period is wet enough, and the winter is not too cold.

Acknowledgements

We are especially gratefull to M. F. De Saintignon, C. Lejeune (Laboratoire d'Environnement climatique, Grenoble), M. Izard (C.E.R.R., Toulouse) and L. Richard (Laboratoire de Biologie Alpine, Grenoble) who provided many climatic data.

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